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# Fooled by savouriness? Investigating the relationship between savoury taste and protein content in familiar foods

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## ABSTRACT

Selecting savoury foods after consuming a protein depleted diet has been suggested to reflect protein seeking behaviour. The modern diet contains a large number of processed foods, many of which are highly savoury to taste, but not necessarily high in protein. The present two studies aimed to investigate the relationship between savoury taste and protein content (actual and participant estimated). Participants (S1  $n = 20$ , S2  $n = 37$ ) completed 100 mm VAS ratings of sensory and nutritional qualities of 18 familiar foods, categorised as sweet low protein, savoury low protein and savoury high protein. In study 2, the individual foods were blended to a fine consistency to disguise their identity and ensure ratings were based primarily on taste. Multilevel linear regression was used to test associations between savoury taste and actual protein content. Protein content did not predict savoury taste rating, irrespective of category. The results also indicated that participants were generally accurate at estimating the protein content of foods, although there was a tendency towards overestimation. The magnitude of this error was increased in low protein savoury foods. Specifically, there was a shift in the spread of estimation scores which showed a greater level of overestimation in some blended compared to unblended foods, and predominantly in savoury foods which participants could not identify. These results provide evidence that savoury taste and protein content are not well linked in the current food environment, but taste may guide nutrient estimations about certain unidentified foods.

## 1. Introduction

Taste is suggested to function as a way of identifying nutrients and avoiding poisons in foods [1]. The taste of a food is therefore thought to be associated with its nutritional content, and a sweet taste is believed to signal the presence of sugars, or carbohydrates in foods [2]. Similarly, dietary protein is positively correlated with savouriness in a variety of commonly consumed foods in the Netherlands [3]. In a further study, savoury taste was moderately associated with protein content in a variety of Australian foods [4]. Additionally, Martin, Visalli [5] created a food-taste database, and note that foods with a higher intensity of savoury taste are also higher in animal protein content. However, a recent study has found weak correlations between a savoury taste and protein content ( $r < 0.3$ ) [6], therefore more research is needed to determine the strength of this relationship. The savoury taste thought to represent protein in foods is the umami taste, which is often defined as “meaty” or “brothy” [7]. The compound which underlies this taste is glutamic acid, an amino acid which is abundant in protein containing foods including meat, fish, dairy and some vegetables [8]. This taste is also elicited by Monosodium

Glutamate (MSG), the sodium salt of the amino acid L-glutamate, which is a savoury flavor enhancer commonly used in both Western and Eastern processed foods and home cooking [35]. It, and the ribonucleotides such as Inosine 5′monophosphate (IMP) and Guanosine monophosphate (GMP), elicit the taste sensation of “umami”.

It has been suggested that humans may use taste-nutrient associations to guide food choices and counteract dietary imbalances. In a dietary intervention study, participants showed a greater preference for savoury high-protein foods after consuming a lower, compared to a higher protein diet [9]. In a further study, reward-related brain activation when exposed to savoury food cues was found to be increased following protein restriction [10]. It is argued that selecting savoury foods after consuming a protein depleted diet may reflect protein-seeking behaviour, and that this could be important for the control of dietary protein intake. It is unclear whether this behaviour is guided by a preference for a savoury taste, or specifically for dietary protein. One study has found that individuals who habitually consume a higher protein diet are more sensitive to an induced protein deficit than lower habitual protein consumers, which is reflected in their increased liking of a high concentration of MSG in this state [11]. This suggests that the

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**Table 1**  
Nutritional composition of study foods.

Category	Food	Macronutrients (g) per 100 g					Energy per 100 g		Percentage of energy		
		Protein	Carbohydrate	Sugars	Fat	Salt	kCal	kJ	Protein	Carbohydrate	Fat
Savoury High Protein	Roast Beef	24.4	1.0	0	2.4	1.0	123	515	79%	3%	18%
	Dry Roasted Peanuts	28.8	9.4	5.3	48.8	1.1	608	2544	19%	6%	72%
	Breaded Ham	23.2	1.2	0	4.0	2.5	134	561	69%	4%	27%
	Chicken Mayonnaise Sandwich	31.0	36.0	2.9	13.1	1.5	400	1674	31%	36%	29%
	Salmon Fillet	23.5	0.5	0	14.9	0.1	228	954	41%	1%	59%
	Mean	26.2	9.6	1.6	16.6	1.2	299	1251	35%	13%	50%
	SD	3.5	15.2	2.4	18.8	0.9	206	862	7%	30%	82%
Savoury Low Protein	Potato Wedges	2.0	22.4	1.0	5.3	0.7	151	632	5%	59%	32%
	Tangy Cheese Doritos	8.2	57.1	3.4	5.3	1.8	510	2134	6%	45%	9%
	Vegetable Spring Rolls	4.8	26.6	5.1	11.1	0.9	230	962	8%	46%	43%
	Sausage Rolls	10.6	20.2	1.0	28.4	1.1	380	1590	11%	21%	67%
	Garlic and Cheese Slices	9.5	35.9	1.8	17	1.1	340	1423	11%	42%	45%
	Crispy Garlic Mushrooms	4.5	20.2	1.2	7.4	0.9	167	699	11%	48%	40%
	Mozzarella Pizza	11.0	26.0	0.0	14.0	0.1	272	1138	16%	38%	46%
	Mean	7.2	29.8	1.9	12.6	0.9	296	1238	10%	40%	38%
	SD	3.5	13.2	1.7	8.2	0.5	139	582	10%	38%	53%
Sweet Low Protein	Toffee Popcorn	1.8	80.3	55.6	9.3	1.4	420	1757	2%	76%	20%
	Jam Ball Doughnuts	4.9	49.6	40	31.8	0	340	1423	6%	58%	84%
	Chocolate and Honeycomb Cheesecake	3.7	33.7	21.5	20.7	1.0	340	1423	4%	40%	55%
	Angel Cake Slice	3.0	59.6	39.2	18.2	0.8	420	1757	3%	57%	39%
	Dried Apricots	4.0	36.0	36.0	0.6	0.1	178	745	9%	81%	3%
	Milk Chocolate Raisins	4.4	69.0	62.0	15.0	0.4	435	1820	4%	63%	31%
	Mean	3.6	54.7	42.4	15.9	0.6	284	1189	5%	77%	50%
	SD	1.1	18.4	14.5	10.6	0.6	163	682	3%	45%	59%

sensing of MSG may be involved in the detection of protein in the diet, particularly when participants habitually consumed higher amounts of protein. Additionally, as humans appear to be able to adapt dietary intake in longer term studies, it has been suggested that they are capable of recognising the macronutrient content of a food [3,11], although it is unclear whether this is based on explicit or implicit knowledge of the protein content of foods.

If selecting savoury foods is associated with appetite for protein, what then underlies this relationship? Rats and hamsters deprived of protein display a preference for a taste which has previously been associated with the nutrient [12,13]. It is argued that humans also have the capacity to form these associations [14], and that learned associations between dietary cues and post-ingestive consequences [15] guide protein appetite. The availability of foods with tastes which are incongruent with their nutritional content could therefore degrade this dietary learning. This is supported by previous research (van Dongen et al. [3]) which found that taste-nutrient relationships may be disrupted by competing tastes within the same food. Psychophysical research has demonstrated that savoury taste can enhance the perception of sweet and salty tastes, and suppress bitterness and sourness [16,17]. A characteristic of many foods in our current dietary environment is the presence of competing tastes. For example, there are “ultra-processed” food products which contain both added salt and sugar [18].

The modern diet contains a large number of processed foods, and it is estimated that in the United Kingdom highly processed foods contribute up to 59% of energy consumed [19]. Here, a highly processed food is defined as a food which has been subjected to industrial processes such as roasting, coating, use of industrial ingredients, salting and heat treatments. Monosodium glutamate, and other savoury flavourings are often used in highly processed foods [20,21]. Many of these foods are highly savoury to taste, but not necessarily high in protein. It has been suggested that humans have a tight physiological control of dietary protein intake, and may overconsume calories to meet absolute protein requirements [22]. This could be of concern, as low protein savoury foods may disrupt protein-seeking behaviour and could contribute to overconsumption of energy and obesity [23]. Although it is important to note that this hypothesis has not been universally supported, and on some low protein diets humans do not

overconsume calories [24]. However, granted that there is a drive to maintain adequate protein intake and that savouriness is used as a cue for protein, the presence of low protein savoury foods in the diet will increase overall energy intake.

Accordingly, the aim of the present studies was to investigate the relationship between savoury taste and protein content across a range of savoury and sweet foods. We were also interested in how much protein these foods are perceived to contain, and whether this is overestimated specifically in low protein savoury foods.

## 2. Study 1

### 2.1. Method

#### 2.1.1. Participants

All participants were recruited through the University of Bristol, School of Experimental Psychology Experimental Hours Scheme, and received one experimental hour's credit in remuneration for their participation. They were sixteen female and four male participants aged 18–22 years ( $M = 19.4$ ,  $SD = 1.3$ ) with a BMI of 18.4–25.1 kg/m<sup>2</sup> ( $M = 21.4$ ,  $SD = 1.7$ ). In study 2, thirty-four female and three male participants aged 18–27 years ( $M = 20.9$ ,  $SD = 2.3$ ) with a BMI of 17.2–27.7 kg/m<sup>2</sup> ( $M = 20.9$ ,  $SD = 2.3$ ) took part in the study. This study was conducted according to the ethical guidelines laid down in the Declaration of Helsinki. Written informed consent was obtained from all participants.

### 2.2. Measures

Participants completed Visual Analogue Scale (VAS) ratings of the sensory and hedonic properties of each food. These comprised a computerised sliding scale ranging between 0 “not at all” and 100 “extremely”. VAS ratings were completed for pleasantness, familiarity, sweetness, savouriness and saltiness, using for example the question “How PLEASANT is the taste of food “x””. The protein, carbohydrate and fat content of each food were also estimated (as a percentage of total energy), using VASs, but only protein estimations are included in analyses. Responses at each end of these latter VASs were anchored

using familiar foods which were not used in the study. To estimate the percentage of protein content, participants were asked “As a proportion of total calories, how high in PROTEIN do you think food “x” is?” with responses anchored from “extremely low, e.g. apple (2% protein)” to “extremely high, e.g. lean turkey (88% protein)”.

### 2.3. Foods

All study foods were bought from J. Sainsbury PLC. The macronutrient compositions of the study foods are displayed in Table 1. Foods were selected based upon their protein content and (expected) savoury taste. Mean energy densities and fat contents were similar between categories. A high protein food was classified as any food above 20 g/100 g protein, based on a median split of protein content of a database of foods varying in macronutrient compositions (see Supplementary Table 1). In study 2 the foods were blended to a fine consistency to disguise their identity and were administered to participants on a spoon.

### 2.4. Procedure

Each participant attended the Nutrition and Behaviour Unit, University of Bristol for a single test session lasting approximately 1 h. They were required to have abstained from eating and from drinking calorie-containing beverages for at least 2 h prior to the study. On arrival, participants read an information sheet and signed a consent form. Participants tasted a single bite from a 50 g portion of each of the 18 foods and completed VAS ratings of their sensory and hedonic properties. Volunteers were instructed to rinse their mouth with and then swallow a sip of water between each food, and were permitted to re-taste foods if necessary to complete the ratings. Each participant received the foods in a different order, according to a balanced Latin Square design. In study 2, participants were asked to state the identity of foods. This was done via a questionnaire administered whereby participants were asked to write down the identity of each food. After all ratings had been completed, age, height and weight were recorded. Participants were debriefed via email once all testing was completed.

### 2.5. Statistical analyses

Statistical power was computed using G\*Power [25], based on an effect size of  $r^2 = 0.31$  for the relationship between protein content and savouriness intensity in highly processed foods (Van Dongen et al. [3]). We calculated that for an alpha of 0.05 a power = 0.8 was achieved with 20 participants. In study 2, to achieve a power = 0.95 with alpha = 0.05, it was estimated that 35 participants were required. Macronutrient composition of foods (g/100 g) was taken from nutrient labels on food packaging. All analyses were performed using R software [26]. A one-way ANOVA was conducted to test for differences in pleasantness and familiarity between categories. This was to check that there were no baseline differences between the categories as this might have confounded the results, for example if participants have a preference for, or are more familiar with some foods compared to others. As participants made multiple ratings and the same food was rated multiple times by different participants the assumption of independence of ratings is violated. Therefore we used a cross classified multilevel model, where ratings are nested within participants and foods, to analyse associations between protein content and savoury taste ratings [27]. The savouriness VAS rating was treated as the dependent variable, and protein content per 100 g and taste category of food (sweet or savoury) as the independent variables. We expected protein content per 100 g to positively predict savouriness VAS rating. However, this was expected to be different between categories, specifically we expected there to be an interaction between taste category of food and protein per 100 g, that is; the low protein savoury category was not expected to have this relationship. The correlation between

estimated protein content and actual protein content was calculated to investigate participants' relative accuracy at estimating the protein content of foods. In study 1, to investigate overestimation of protein content in low-savoury foods, estimated protein content was subtracted from actual protein content to calculate an error score. A one-way, Category (sweet low protein, savoury low protein, savoury high protein) ANOVA, based on a multilevel model was used to test for differences in error scores between categories. Estimation scores from study 2 were compared to study 1 to further investigate whether there is a greater degree of overestimation of low protein savoury foods when they are visually unidentifiable. As each foods “actual protein” lies somewhere different along the VAS, each has a different potential overestimation value, which could make statistical comparisons between foods difficult to interpret. Therefore, additional results for protein estimation per food are presented as boxplots. In study 2, responses to the food identity questionnaire were coded as correct or incorrect by two independent raters and then compared. A response was considered to be correct if it was largely within the correct category of food, i.e. “cake” instead of “angel cake”, or “nuts” instead of “peanuts”.

## 3. Study 1 results

### 3.1. Pleasantness and familiarity of foods in study 1 and 2

Pleasantness and familiarity ratings of foods from study 1 and 2 are summarised in Table 2. One-way ANOVA indicated that there were no significant differences between categories in terms of pleasantness  $F(2,357) = 1.76$ ,  $p = 0.18$ , or familiarity  $F(2,357) = 1.16$ ,  $p = 0.32$  for study 1. There was a significant difference between categories in pleasantness ratings  $F(1,627) = 27.96$ ,  $p < 0.001$  for study 2. Tukey adjusted post-hoc tests indicated a significant difference between sweet low protein and savoury low protein ( $p < 0.001$ ) and savoury high protein categories ( $p < 0.001$ ), but no significant difference between savoury high and low protein ( $p = 0.901$ ). There was also a significant difference between categories for familiarity ratings  $F(1,627) = 19.41$ ,  $p < 0.001$ , and Tukey's post-hoc tests indicated a significant difference between sweet low protein and savoury low protein ( $p < 0.001$ ) and savoury high protein ( $p < 0.001$ ) categories. There were no significant differences in familiarity ratings between savoury high and low protein ( $p = 0.95$ ).

### 3.2. Relationship between protein content and savoury taste rating

#### 3.2.1. Cross-classified multilevel model

Mean savouriness ratings for each category are summarised in Table 2. An intercept only model was fitted to the data first to investigate the percentage of variance on the participant and food level. This model and the multilevel regression model is reported in Supplementary Table 2 and corresponding data are shown in Fig. 1. Considering the difference in variance between the intercept-only model

**Table 2**  
100 mm pleasantness, familiarity and savouriness ratings of study 1 and 2 foods.

	Category	100 mm VAS rating					
		Pleasantness		Familiarity		Savouriness	
		M	SE	M	SE	M	SE
Study 1	Sweet Low Protein	70	3	69	2	24	2
	Savoury Low Protein	73	2	68	2	76	1
	Savoury High Protein	75	3	63	2	68	2
Study 2	Sweet Low Protein	70	2	80	2	25	2
	Savoury Low Protein	55	2	65	2	77	1
	Savoury High Protein	54	2	66	2	75	1

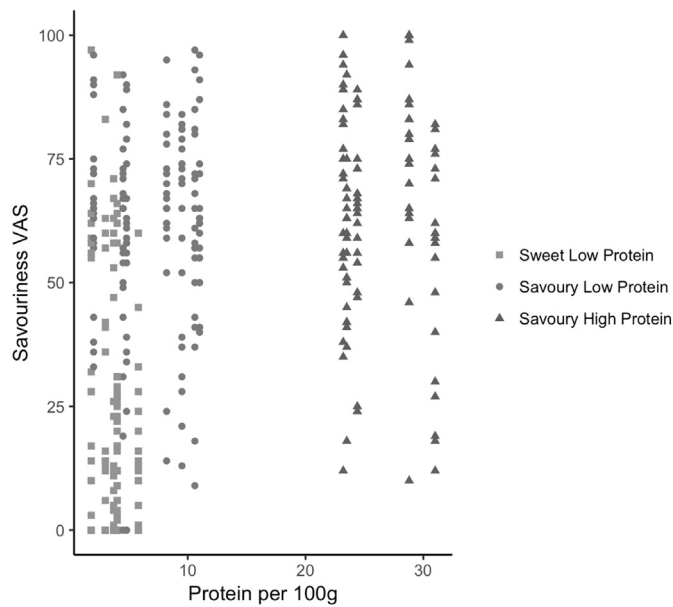


Fig. 1. Relationship between protein content per 100 g and savouriness VAS rating. Note: each point on the graph represents one participant rating of one food.

and the cross-classified model, this shows that adding predictors reduced the food-level variance by 55%. The cross-classified multilevel model indicated that the only significant predictor of savouriness rating was whether the food belonged to a savoury category as opposed to sweet category. Protein content per 100 g was not associated with savouriness VAS rating. There were also no significant interactions between protein per 100 g and category of food, indicating that this relationship does not differ based on category membership.

### 3.3. Protein estimation

Protein estimation errors are summarised in (Fig. 2). A one-way ANOVA, based on a multilevel model indicated that protein content of foods was overestimated for all categories,  $F(1,338) = 74.48$ ,  $p < 0.001$ . The error score was also non-significantly different between categories  $F(2,338) = 32.58$ ,  $p = 0.07$ , Tukey's post-hoc tests indicated that there was a marginally non-significant difference between savoury low protein and savoury high protein ( $p = 0.07$ ,

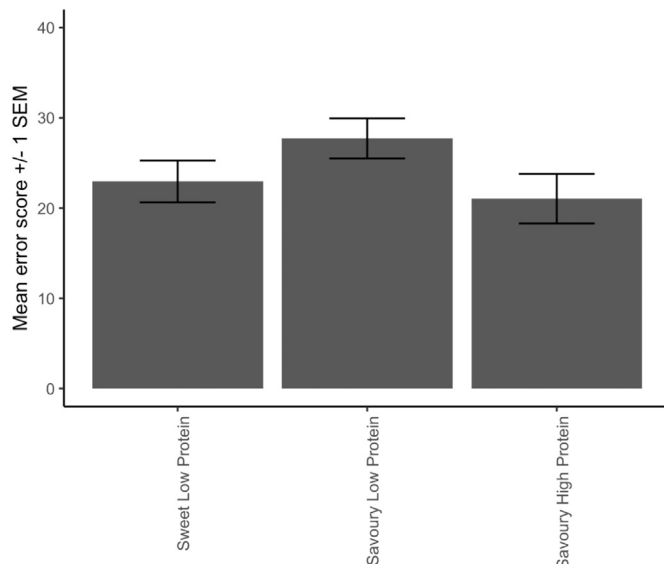


Fig. 2. Graph showing protein estimation error score for each category.

$d = 0.24$ ), but no difference between savoury low and sweet low Protein ( $p = 0.23$ ,  $d = 0.18$ ) and savoury high protein and sweet low protein categories ( $p = 0.82$ ,  $d = 0.07$ ). There was a significant correlation between actual protein content and estimated protein content across all foods ( $r = 0.68$ ,  $p < 0.001$ ).

## 4. Interim discussion

The results of study 1 indicate that protein content is not a significant predictor of savoury taste rating, in this set of foods. The results show that participants overestimated the protein content in foods from all categories. However, this was no different between categories. This error was greatest for savoury low protein foods compared to sweet low protein foods. It must be noted that the results may have been influenced by the familiarity of the foods used, which may have led participants to use prior knowledge about the foods' nutrient content to make their ratings, as opposed to relying solely on the taste of the foods. Therefore, the aims of study 2 were first, to investigate whether these results would be replicated and second, to explore whether participants would overestimate the protein content of low protein savoury foods when they are visually unidentifiable.

## 5. Study 2 results

### 5.1. Relationship between protein content and savoury taste rating

#### 5.1.1. Cross-classified multilevel model

The intercept only and cross-classified multilevel regression model is reported in Supplementary Table 3, and corresponding data are shown in Fig. 3. The difference in variance between the intercept-only and cross-classified model indicate that adding predictors to the model reduced the food-level variance by 59%. The analysis indicated that the only significant predictor of savouriness rating was whether the food belonged to a savoury category as opposed to sweet category. Protein content per 100 g was not associated with savouriness VAS rating. There were also no significant interactions between protein per 100 g and category of food, indicating that this relationship does not differ based on category membership.

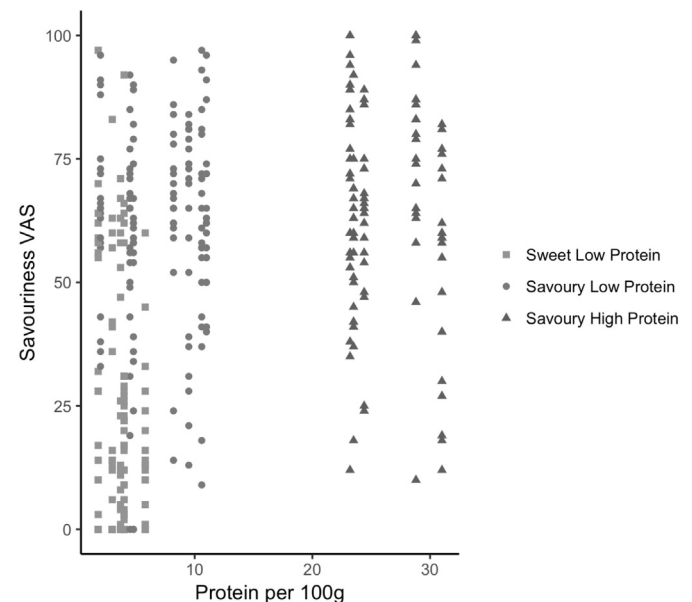


Fig. 3. Graph showing relationship between protein content per 100 g and savouriness VAS rating for each category. Note: each point on the graph represents one participant rating of a food.



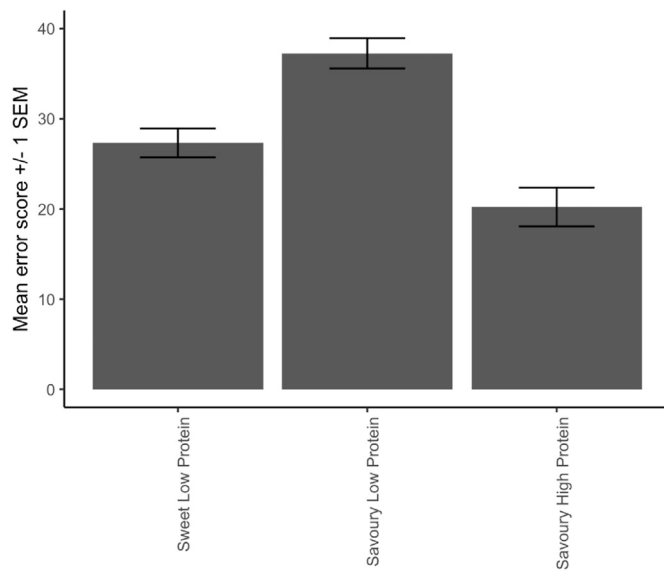


Fig. 4. Graph showing protein estimation errors between categories for blended foods.

## 5.2. Protein estimation

Protein estimation errors are summarised in Fig. 4. A one-way ANOVA indicated that the error score was significantly different between categories for blended foods,  $F(2,627) = 24.82$ ,  $p < 0.001$ . Participants overestimated the protein content of all foods,  $F(1,627) = 337.64$ ,  $p < 0.001$ . Tukey's post-hoc tests indicated that there was a significant difference between savoury low protein and sweet low protein categories ( $p < 0.001$ ,  $d = 0.39$ ), and a significant difference between savoury low protein and savoury high protein ( $p < 0.001$ ,  $d = 0.60$ ), and a significant difference in error scores between savoury high protein and sweet low protein categories ( $p = 0.01$ ,  $d = 0.26$ ). There was also a significant correlation between estimated and actual protein content of foods ( $r = 0.59$ ,  $p < 0.001$ ). Figs. 5–7 show the spread of estimation scores, compared between study 1 and study 2. In both the savoury high protein and sweet low protein category, the spread of estimation scores are similar between the two studies. This is also the case for the majority of foods in the savoury low protein category. The only food which shows a marked increase in

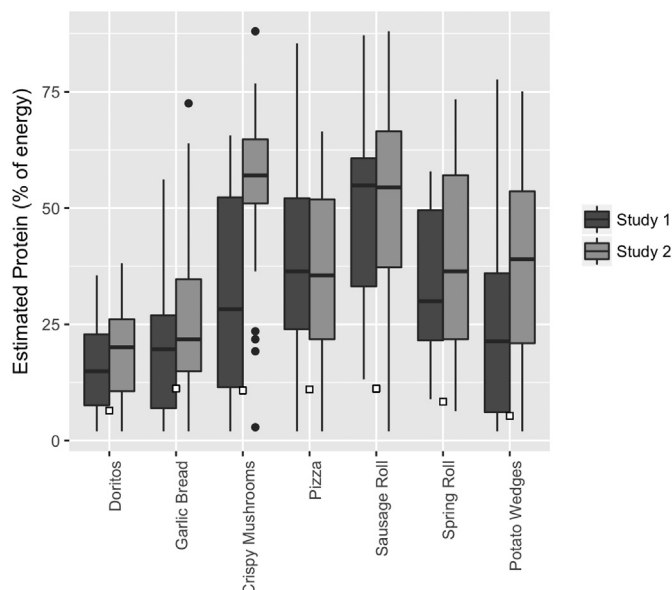


Fig. 5. Boxplot showing spread of estimation scores for savoury low protein category.

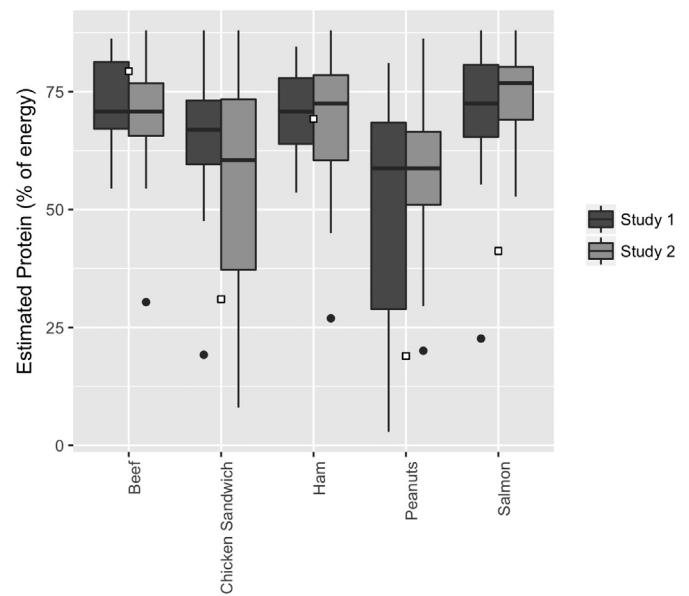


Fig. 6. Boxplot showing spread of protein estimation scores for foods in the savoury high protein category.

Note. Description of box and whisker plots are included in the caption to Fig. 5.

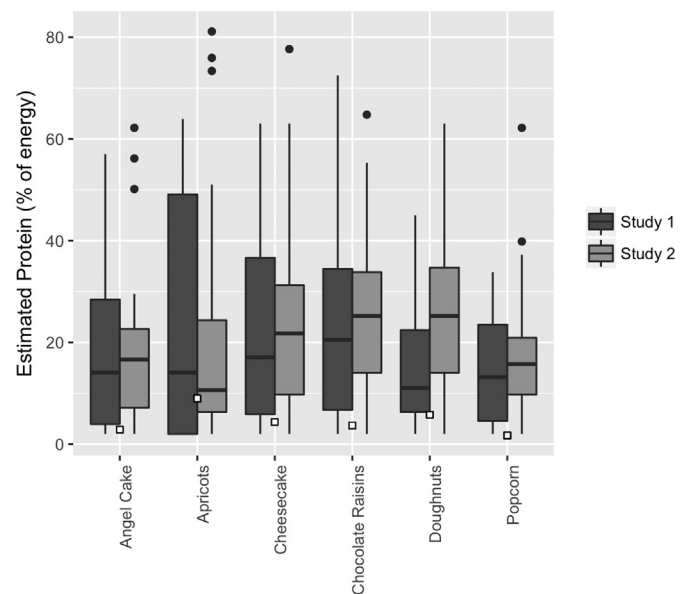


Fig. 7. Boxplot showing spread of protein content estimation scores for sweet low protein category.

Note. Description of box and whisker plots are included in the caption to Fig. 5.

protein estimation is crispy garlic mushrooms, which is also the food which no participant in study 2 was able to identify explicitly (see Table 3).

Note: for all figures, white square indicates actual percentage of energy as protein for each food. Food names have been shortened for graph labels. The line represents the median, and the upper edge of the box represents the 75% quantile, and the lower edge represents the 25% quantile. The upper end of the whisker represents the largest observation, and the lower end represents the smallest. Black dots are used to represent outliers.

## 6. Discussion

The results of the present studies indicate that protein content does not positively predict savoury taste rating. This relationship is not

**Table 3**  
Proportion of participants who correctly guessed the identity of each food.

Category	Food	% of participants correct
Savoury High Protein	Roast Beef	68
	Dry Roasted Peanuts	97
	Breaded Ham	65
	Chicken Mayonnaise Sandwich	38
	Salmon Fillet	97
Savoury Low Protein	Potato Wedges	35
	Tangy Cheese Doritos	92
	Vegetable Spring Rolls	30
	Sausage Rolls	19
	Garlic and Cheese Slices	89
	Crispy Garlic Mushrooms	0
	Mozzarella Pizza	19
	Toffee Popcorn	100
Sweet Low Protein	Jam Ball Doughnuts	30
	Chocolate and Honeycomb	65
	Cheesecake	
	Angel Cake Slice	59
	Dried Apricots	92
	Milk Chocolate Raisins	97

different when the food is from a low savoury or sweet category. The foods used in the study also confirm that there are indeed foods which are highly savoury to taste, but not necessarily high in protein. Despite an overall tendency towards overestimation, a positive correlation between actual and estimated protein content suggests that the participants generally had good knowledge about protein content of foods. Participants overestimated the protein content of foods from a low protein savoury category more than from high protein savoury or low protein sweet categories, when they were blended. Although only seen in one food (crispy garlic mushrooms), a shift in protein estimation errors may suggest that when faced with an unidentified savoury food, participants believe it is higher in protein than it actually is.

These results correspond to a recent study using a trained sensory panel, which showed weak relationships between umami taste and protein [6]. However, these results do not confirm other previous research [3,4] which found protein content to be positively associated with savoury taste rating in a variety of foods. As well as using a different set of test-foods, two key differences in study design may explain this discrepancy in results. First, van Dongen et al. [3] used a trained sensory panel to rate savouriness taste intensity, whereas the present study used naïve participants. It may be suggested that a trained sensory panel is more accurate at detecting the individual components of foods, e.g., glutamic acid. Second, the studies [3,4] found that the relationship between protein content and savoury taste was less pronounced in highly processed, compared with raw and moderately processed foods. A further explanation of the difference in results could therefore lie in the fact that the clear majority of foods in the present studies could be defined as highly processed [19]. This may lead to competing tastes within the same food and thus disrupt the taste-nutrient relationship. The crispy garlic mushrooms would also be high in umami taste compared to the other foods, which could account for the overestimation of their protein content in blended form. Blending also may have changed the sensory properties, specifically the texture of the foods. If highly processed foods already contained competing tastes, for example, through added sugar, salt and savoury flavourings, the blending process may have accentuated this. Additionally, the blended versions of foods were also rated as lower in palatability than their unblended counterparts. Time spent in the oral cavity could also influence the processing of umami from taste receptors to the gut and brain. Post-ingestive consequences may also be important as umami detectors also exist in the gut and therefore the sensing of protein may be worse if the product is liquefied and spends less time in the gut.

We relied on participants' own understanding of the definition of savoury. The word savoury was chosen based on an expectation that

this would be more commonly understood than umami by our participants. Osawa and Ellen [28] investigated the cultural specificity of taste terminologies and found that British participants had difficulty in describing the umami taste, but did use descriptors such as “savoury and salty like boullion and oxo cube” to describe the taste of umami solutions, suggesting that they do understand the word “savoury”. This was explored further by calculating correlations between savouriness and saltiness ratings. Whilst correlated (study 1:  $r = 0.47$ ,  $p < 0.001$ , study 2:  $r = 0.67$ ,  $p < 0.001$ ), this is not a one-to-one relationship, which suggests that participants understand savouriness and saltiness as related, but nonetheless substantially separate constructs.

It is possible that different types of umami taste could have affected the present results. The umami taste can be elicited by both MSG and ribonucleotides such as IMP and GMP. It has been noted that nearly all protein containing foods contain glutamate (MSG), whereas IMP is found primarily in meat and some types of fish (Luscombe-Marsh et al. [7]). Therefore, being mostly meat and fish products, the high protein savoury products in the present studies would have primarily contained IMP and MSG, whereas the low protein savoury products GMP and MSG (or just MSG). It is therefore possible that it is the presence of IMP alongside MSG which signals the presence of protein in a food [29]. Research has shown that IMP and MSG together increases preference for foods more than MSG alone [30]. However no research to date has investigated how MSG and IMP together are involved in a protein-signalling effect.

Previous research [4] has also found saltiness to be positively associated with protein content. This was explored further by applying the same multilevel regression model to the data using saltiness as the dependent variable instead of savouriness (see Supplementary Table 4). Data from study 1 and 2 were both included in this model, as there is no reason to expect the relationship would be different in the two studies. Results indicated that protein per 100 g is not a significant predictor of salty taste. We may therefore conclude that in this set of foods at least, protein content is not well linked with savoury or salty taste perception.

It is unclear whether our sample would have a better, or worse understanding of the macronutrient compositions of foods than the general population. Undergraduate students stereotypically consume an unhealthy diet [31], so may exhibit less knowledge about nutrient compositions of foods. However, the majority of participants in this study were young females, who may be preoccupied with weight management [32]. This may lead to greater knowledge about the nutrients a familiar food contains. It would be of interest to repeat this study in a sample more representative of the general population, or at least take a measure of nutrition knowledge (for example). Additionally, in the current study we did not select our participants based on dietary restraint or other psychological variables. It would therefore be of interest to repeat this research using different populations with potentially differing levels of nutritional knowledge, including restrained versus unrestrained eaters and trained versus untrained consumers.

By asking participants to estimate a food's protein content as a proportion of calories relies on them also having knowledge about its overall calorie, plus fat and carbohydrate content. For example, peanuts contain a large amount of protein by weight (28 g/100 g), however as a proportion of energy, their protein content is relatively low (18.9% energy-as-protein), due to their high fat content. However, this could be arguably more realistic than simply asking for the number of grams of each nutrient, as nutrients do not exist in isolation within a food [33]. Future research should therefore aim to identify calorie literacy to ensure participants responses are based on an understanding of calories.

The conclusions from the present study may seem in conflict. If dietary protein is not related to savoury taste ratings, then why would the protein content of an unidentified savoury food be overestimated? As participants are relatively accurate at estimating the protein content of this set of foods, these estimations may usually be based upon explicit knowledge based on the identity of the foods. When presented with an

unidentified savoury food, other strategies may be employed to estimate protein content, which could rely more on the presence of a savoury taste. This is exemplified by the finding that the greatest shift in overestimation of protein was for crispy garlic mushrooms. They were rated as highly savoury, and were the only food to not be explicitly identified in its blended form. However, based as it is on a single food, this finding warrants further investigation.

If savoury taste and dietary protein are not well linked in the current food environment, then what underlies the high estimate of protein content for this particular food (crispy garlic mushrooms)? This may also suggest that ordinarily participants do not associate mushroom with protein, but in its blended and unrecognisable form, the umami taste may serve as a predictor for protein content. One potential explanation is that the association between protein and savoury taste is not learned, but rather this overestimation of an unidentified food is based upon an innate link between protein and savoury taste. Neonates display a facial reaction of acceptance towards umami taste solutions [34]. This is comparable to the facial expression in reaction to a sweet taste, and a sweet taste has been reliably linked to the sugar content of a food [3]. As neonates accept an umami taste from birth, this may signal an basic understanding that glutamate is a signal for protein.

If there is a drive to maintain adequate protein intake, one important question concerns how protein is identified in the diet. This could be explicitly, or implicitly via knowledge of the protein content of foods, or other cues not measured in these studies. As there was evidence that participants do have a general ability to recognise the protein content of foods, this may guide appropriate selection. However, if a drive for protein does increase desire for savoury foods, and low protein savoury foods are consumed, there is a risk of overconsumption of energy. Previous research (e.g. [9,10]). has suggested that participants choose more savoury foods after a lower protein diet. The present findings may be relevant to understanding these results, and may suggest that this increased choice of savoury foods reflects an unconscious understanding that protein could be signalled by a savoury taste. However, the results also indicate that due to the foods available in our current environment, this may not be a useful strategy for maintaining protein intake, as savoury taste is not reliably correlated with protein content. This may have implications for weight management and obesity.

## 7. Conclusion

In the set of foods tested, protein content was not well linked to savoury taste. It may be suggested that since the foods in the study were highly familiar, this conclusion can be extended to the modern food environment in general, at least as it exists in the UK. Results for estimated protein content compared between blended and unblended foods suggest that when faced with a completely unidentified savoury food (crispy garlic mushrooms), participants overestimate the protein content of that food. Thus, the present studies demonstrate that one can be “fooled” by savouriness, to the extent that protein content is not predicted by savoury taste. These results may have implications for the mechanisms underlying control of protein intake, if indeed this is physiologically tightly controlled.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.physbeh.2018.03.009>.

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